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A NEW GENUS AND SPECIES OF PHYLLOTINE RODENT (MAMMALIA: MURIDAE) FROM NORTHWESTERN ARGENTINA

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Abstract

Andalgalomys, a new (Recent) genus of phyllotine rodent is described. Included species are *A. olrogi*, a new species from the *Larrea* desert of the Bolsón de Pipanaco, Catamarca Province, Argentina, and *A. pearsoni* (Myers), which is reassigned from the genus *Graomys*. *Andalgalomys* is considered to be most closely related to *Calomys* and *Eligmodontia*, and is somewhat intermediate to *Calomys* and *Graomys* in a linear arrangement. Dental and cranial features of *Andalgalomys* are especially close to *Calomys*, with *A. pearsoni* exhibiting more primitive features and a closer similarity to *Calomys* than *A. olrogi*. *A. pearsoni* is considered to be quite similar to a generalized Chacoan ancestral form, and lives today in intersylvan grassland refugia in the Paraguayan Chaco. *A. olrogi* is specialized for a desert habitat, exhibiting bullar enlargement, lateral digit reduction, and lengthening of its appendages. The karyotype of *A. olrogi* consists of a $2n$ of 60, with 116 autosomal arms. The X-chromosome is a large submetacentric, and the Y is a small submetacentric. This karyotype is the most divergent among the phyllotines, but can be derived from that of *Calomys sorellus* by pericentric inversions.

Introduction

Phyllotine rodents are a South American group of primarily pastoral cricetines, which are allied in an informal, but seemingly natural

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grouping of from seven (Hershkovitz, 1962) to eleven (Pearson and Patton, 1975) or more genera. The phyllotines are better known taxonomically than other South American cricetines, the species of the group having been reviewed by Hershkovitz (1962). Additionally, Pearson's (1958) revision of the genus *Phyllotis*, and Pearson and Patton's (1975) report on the karyology of phyllotines have added greatly to our understanding of the relationships of the phyllotine genera. Although much remains to be learned about the systematics of phyllotines, the group composition and intragroup interspecific relationships are becoming increasingly clear. In this paper, we follow the clustering of Sigmodontini species as set forth by Pearson and Patton (1976) and Gardner and Patton (1976).

Phyllotines are included within the tribe Sigmodontini, subfamily Cricetinae, of the family Muridae (Hershkovitz, 1966). The phyllotine species have complex penes, with the distal cartilagenous portion of the bacula being tridigitate. Penis and baculum morphologies among phyllotines are quite diverse, and the differences between phyllotine genera are as great as the differences among the Sigmodontini groups with complex penes (that is, the akodonts, oryzomyines, phyllotines, and sigmodonts, Hooper and Musser, 1964). The Sigmodontini form an adaptive complex that encompasses aquatic, subfossorial (including the adaptively similar grass-tunneling voles), scansorial, and arboreal species. Overall, these four groups are little differentiated morphologically, and both intragroup and intergroup parallelism and convergence are common. Furthermore, some apparently annectent forms between groups and between genera within groups compound the difficulties of arranging a satisfactory taxonomy.

Phyllotines are most diverse in grasslands, scrublands, deserts, and arid Andean highlands. They occupy semitropical deciduous forests, and are uncommon in palustrine habitats. The majority of species are scansorial, some are vole-like in habits and appearance, and a few (for example, *Graomys*) are somewhat arboreal (Mares, 1973, 1976). Overall, phyllotine species richness is low in lowland desert and semidesert habitats, and most species are associated with rock-scrub habitats of upper bajadas or xeric montane ecosystems. *Eligmodontia typus* and *Phyllotis gerbillus* are the most desert-adapted phyllotine species. The former is widespread in dry steppe, desert, and puna habitats in the Andes and intermountain valleys of Argentina, Chile, and Bolivia, and in southern Peru. The latter is apparently confined to the Sechura Desert of northwestern Peru (Hershkovitz, 1962; Mares, 1973; Pearson, 1972). *E. typus* has the most pronounced morphological adaptations to a desert habitat, possessing spade-shaped, gerbil-like hind feet, with single, large, hirsute cushions on the soles (Hershkovitz, 1962). However, the external pinnae and auditory bullae are only moderately enlarged, and are less noteworthy than those of the rock and scrub inhabitants, *P. amicus*, *P. boliviensis*, and *Graòmys griseoflavus*. Both lowland desert species are fairly well-adapted, physiologically, to desert life (Koford, 1968; Mares, 1975, 1977*a*).

It surprised one of us (Mares), during field studies in the desert of Catamarca Province, Argentina, to discover that a mouse just removed from a livetrap (and presumed to be *E. typus*) had no hairy pads on the hind feet. Unfortunately, this discovery came during actions ancillary to specimen preparation, and although it was presumed at that time to be a new species, three and one-half years elapsed before four additional specimens were captured and chromosome data were secured. Examination and comparison of the five specimens with all other remotely similar South American rodents convinced us that this form had no known close relatives, but was allied with the phyllotines. Superficially, the specimens are very similar to the sympatric *E. typus*. However, they differ in numerous details, most notably in their naked-soled, cushionless feet, greatly inflated auditory bullae, and their different molar cusp patterns. Most surprising, however, is the striking similarity of these specimens in external and cranial details to some of the Old World gerbillines.

Subsequent to the discovery of this new form, and prior to its description here, Myers (1977) described a new species of phyllotine (*Graomys pearsoni*) from the dry grassland islands in the Chaco of western Paraguay. Our analyses lead us to the conclusion that *G. pearsoni* and the new species from Catamarca Province, Argentina, are most closely related and together comprise a new genus.

METHODS

Somatic chromosomes of bone marrow cells were prepared using the colchicine, hypotonic sodium-citrate technique of Patton (1967). Karyological nomenclature is as defined by Patton (1967). The specimens examined cytologically are listed in the description of the new species.

Phalli were prepared using the techniques outlined by Lidicker (1968). However, 6 to 8 h were sufficient for clearing the dry phalli in 2% KOH, and a day's stay (as little as 12 h) resulted in disintegration of the soft tissues. Also, a few drops of 2% KOH, added to the alizarin solution, hastened the staining of the osseous material. Terminology and measurements of phalli are as defined by Hooper and Musser (1964).

Fifty-one dental characters were evaluated qualitatively for each specimen of the new genus, and for five specimens each of *Calomys callosus*, *Eligmodontia typus*, and *Graomys griseoflavus* (see list of specimens examined). Also, the same characters were evaluated for at least one each of the other species listed in the "specimens examined." These dental traits are primarily those utilized by Hershkovitz (1962) in defining the genera and species of phyllotines. Those, and others found useful by us in distinguishing genera and species, are presented in the formal descriptions and, unless otherwise indicated, are as defined by Hershkovitz (1962). In addition, thirty-nine external and cranial traits were measured. These morphometric characters are listed in Table 1, and are as illustrated by Hershkovitz (1962) or defined by DeBlase and Martin (1974), except for the following.

Interparietal length.—Greatest length of the interparietal bones, measured at, or near, the midpoint on the cranium.

Rostral width.—Greatest width across the rostrum at a point immediately anterior to the zygomatic processes.

Incisive foramen length.—Greatest length of the incisive foramen; where the two foramina were asymetrical, the longer of the two was measured.

Distance between molar rows.—Least distance between the upper molar rows, measured from the lingual sides of the molars.

Parapterygoid fossa width.—Width across the parapterygoid fossa, measured from the outer edge of the pterygoid process to the outer rim of the parapterygoid fossa. This measurement was taken at the midpoint of the fossa.

Mesopterygoid fossa width.—Width between the pterygoid processes, measured in the same plane as the parapterygoid fossa width.

Number of palatal foramina.—A count of the foramina on the palate between, and including, the posterior palatal foramen and the anterior palatal foramen. In most species, the numbers differ on the right and left sides, so the two sides were scored separately.

Incisive foramen intrusion.—The anterior-posterior distance that the incisive foramina extend between the molar rows.

Length of molars.—The greatest length of each of the molars, measured from occlusal view. In species with molars that are excessively tilted in an anterior-posterior plane, the first upper molar was measured from labial view.

Univariate statistical analyses included standard statistics and Student's *t*-tests of samples of the new genus. Multivariate analyses were preformed using a stepwise discriminant function program (BMD07M, Dixon, 1976) and numerical taxonomic programs (MINT). The discriminant function program performs multiple group discriminant analyses, utilizing linear classification functions. Squared Mahalanobius distance statistics (D^2) and canonical analysis are also included in this program. Average Euclidean distance (taxonomic distance) coefficients, and Q-mode correlation (similarity) coefficients were calculated using the MINT programs. Data were standardized in the MINT programs, and phenograms were constructed by the unweighted pair-group method using arithemetic averages.

SPECIMENS EXAMINED

All specimens used in the morphometric analyses were young adults or older. In addition to the specimens that were used in the multivariate and/or qualitative analyses and which are listed below or beyond, hundreds of specimens, representing most South American cricetine species, and including all of the *Graomys* holotypes (but excluding *G. pearsoni*), were examined and compared with the new form. All of the specimens listed are preserved as standard skin and skull preparations, and are deposited in the Carnegie Museum of Natural History (CM) unless they are designated as being housed elsewhere. Specimens with the acronym AMNH are in the American Museum of Natural History, and those designated UCONN are deposited in the University of Connecticut Museum of Natural History. The initials BM designate the British Museum of Natural History.

Akodon varius Thomas.—ARGENTINA. *Tucumán*: Horco Molle, 20 km NW San Miguel de Tucumán (5).

Andinomys edax Thomas.—ARGENTINA. *Tucumán*: Horco Molle, 15 km W San Miguel de Tucumán (3).

Auliscomys sublimis Thomas.—ARGENTINA. *Salta*: along Highway 40, S of junction of Highways 40 and 51, 4,100 m (1).

Calomys callosus (Rengger).—ARGENTINA. *Tucumán*: Horco Molle, 25 km NW San

Miguel de Tucumán (1); Quebrada de Lules (below dam), 8 km SW San Pablo (4).

Calomys muriculus (Thomas).—BOLIVIA. *Santa Cruz*: Santa Cruz de la Sierra (1); Puerto Suarez (1).

Calomys musculinus (Thomas).—ARGENTINA. *Catamarca*: 10 km (by road on Route 62) W Andalgalá (1).

Eligmodontia typus Cuvier.—ARGENTINA. *Catamarca*: 1.5 km S Andalgalá (1); 6 km N Saujil (1). *Mendoza*: 31 km W (by El Manzano Rd) of Tunuyán (2). *Tucumán*: 45 km S Cafayate, along Highway 40 (1).

Graomys edithae Thomas.—ARGENTINA. *Catamarca*: Otro Cerro, about 18 km NNW Chumbicha (1), BM.

Graomys domorum (Thomas).—ARGENTINA. *Salta*: 11 km N Anta (1). BOLIVIA. *Cochabamba*: Parotani, 8,800 ft (4), AMNH.

Graomys griseoflavus (Waterhouse).—ARGENTINA. *Catamarca*: Rio Andalgalá, immediately N Andalgalá (5). BOLIVIA. *Santa Cruz*: Campos de Guanacos (5).

Holochilus brasiliensis (Desmarest).—ARGENTINA. *Formosa*: Estancia Santa Catalina, approximately 5 km W Cogoy, Departamento de Patiño (1).

Oryzomys albigularis (Tomes).—COLOMBIA. *Magdalena*: Sierra del Libano (1). *Santander*: Peña Blanca (1). BOLIVIA. *Cochabamba*: Incachaca (2).

Oryzomys capito (Olfers).—ARGENTINA. *Salta*: 24 km NW Agua Blanca, Departamento Orán (1).

Oryzomys longicaudatus (Bennett).—ARGENTINA. *Catamarca*: Rio Andalgalá, immediately N Andalgalá (4); La Toma, 6.5 mi N Andalgalá (1).

Oxymycteris paramensis Thomas.—ARGENTINA. *Salta*: 24 km NW Agua Blanca, Departamento Orán (1).

Phyllotis darwini (Waterhouse).—ARGENTINA. *Catamarca*: along Rio Potrero, 10 km (by road) N Potrero (1); Hills at E end of La Puntilla (2). *Cordoba*: La Cumbre, en Estancia de la Loma, approximately 1 km from Estancia el Rosario (1). *Tucumán*: Horco Molle, 15 km W San Miguel de Tucumán (1).

Phyllotis micropus (Waterhouse).—CHILE. *Llanquihue*: Rio Nireguao (1).

Phyllotis osilae J. A. Allen.—ARGENTINA. *Tucumán*: El Infiernillo, 18 km NW (by road) Tafí del Valle (2); El Infiernillo, 19 km NW (by road) Tafí del Valle (1).

Reithrodon physodes (Olfers).—CHILE. *Llanquihue*: Rio Nireguao (1).

Zygodontomys lasiurus Thomas.—BRAZIL. *Pernambuco*: Exu (1).

DESCRIPTIONS

Andalgalomys, new genus

Type species.—Andalgalomys olrogi, new species.

Included species.—Andalgalomys olrogi, new species; *Andalgalomys pearsoni* (Myers).

Diagnosis.—A member of the tribe Sigmodontini, subfamily Cricetinae, of the family Muridae; most closely allied with the phyllotine species. Size moderately small, with slightly to moderately haired and pencilled tail; tail longer than head-body length; pinnae moderately large and sparsely covered with fine hairs; soles of feet naked. Skull with divergent (posteriorly) interorbital region; supraorbital region ledged; nasals slender and straight; molar rows parallel; palatines with large slits usually present; parapterygoid fossa border ledged anteriorly and medially; bullae relatively greatly inflated. Molars brachydont, their crowns tuberculate and slightly crested, with some tendency toward lamination in the upper molars. M^1 with well-developed anterior median fold and an anteromedian style; postcingulum with a slight notch or fold. M^2 anteroloph small, and directed nearly anterior. Major fold of M^3 deep, dividing the metacone-hypocone from the protocone-paracone by a double enamel wall that usually persists in worn teeth. Procingulum of M_2 not evident, and anteroconulid not apparent. Baculum tridigitate, the medial digit shorter than the lateral digits, and curved slightly dorsad; lateral digits robust; proximal end of baculum expanded laterally, and straight edged; distal end slightly expanded and ball-shaped; bacular mounds extend beyond glans hood. Glans penis as long as, or longer than, baculum.

Etymology.—This genus is named for the village of Andalgalá, near which the type species was captured, and of which the authors have fond memories.

Description.—Size moderately small (see Table 1). Tail longer than head-body length, and sparsely to moderately haired, the hairs at the tip forming a very slight (<3 mm beyond tip) to moderate (5–9 mm) pencil. Ear pinnae well developed and sparsely haired. Pelage of moderate length (hairs on rump 5–10 mm) and of soft texture. Feet with naked soles; hind feet with six plantar tubercles (Fig. 4); first hind digit small, not, or barely (claw tip only) reaching the base of the second digit; hind digits 2 to 4 somewhat elongated.

Skull with moderately inflated braincase, slightly narrower than the zygomatic width. Interparietals broad, extending the width of the dorsal cranial surface; their length short. Sides of supraorbital region with overhanging ledges that extend as ridges onto the temporal region; interorbital region moderately constricted, being about the same width as the rostral width; interorbital region evenly divergent posteriorly (wedge shaped). Zygomatic arches only slightly convergent anteriorly; the anterior border of the zygomatic plate slightly concave. Premaxillae barely encroaching on the dorsal surface of the rostrum, except at the premaxilla-frontal suture. Nasals straight, not noticeably divergent or convergent anteriorly, and relatively narrow; nasals concave, forming a shallow, longitudinal depression dorsally. Infraorbital foramen deeply notched dorsally. Incisive foramina narrow and extending to about the level of the first molars. Palate long and of moderate width; anterior palatal foramen coalesced with other palatine foramina to form a long slit (or infrequently present as small, independent foramina of variable number). Bullae greatly inflated compared to other phyllotines. Parapterygoid fossa width more than twice as great as the mesopterygoid fossa width, measured in the same plane; fossa moderately deep; anterior and medial borders of the parapterygoid fossa with a prominent shelf or ledge. Posterior border of mandible deeply notched; coronoid process small; condyloid process narrower than, or equal to, the greatest width of the angular process.

Upper incisors slender, opisthodont, their anterior faces smooth; upper molar rows parallel-sided, somewhat bowed outwardly medially; molars brachydont, their cusps tuberculate and crowns slightly crested; anterior enamel walls of upper molars slightly more projecting than the posterior enamel walls, both inclined posteriorly and somewhat rotated inwardly; the principal cusps of the outer side arranged either opposite or slightly in echelon to those of the inner side; upper molars with some tendency toward lamination, their cusps subovate to somewhat triangular in outline.

M^1 with well-developed anterior median fold, the procingulum bilobate, forming a larger anterolabial conule and a smaller anterolingual conule; anteromedian style on anterior surface of procingulum varies from obsolete (barely discernable) to well developed, but usually readily apparent; procingulum ovate in outline; postcingulum usually with a slight fold or notch; second secondary fold absent; mesostyle present or absent, when present, it is very tiny; anteroconule present or absent; anterolabial style present and well developed, or obsolete and represented only by a small shelf.

M^2 with small anteroloph directed nearly anterior; first primary fold shallow, but complete (not an island); second secondary fold absent; first minor fold small and directed in an anterior-posterior plane; postcingulum usually not apparent; metacone greater than or equal to hypocone in size; paracone greater than or equal to protocone in size; second internal fold complete (not an island).

M^3 with an obsolete (rarely) or without an anteroloph; first primary fold obsolete (rarely) or absent; second secondary fold absent; major fold deep, usually completely dividing the protocone and paracone from the metacone and hypocone by a double enamel wall, even in moderate to well-worn teeth; postcingulum not evident.

M_1 with well-developed procingulum; anterior median fold forming a shallow notch (or rarely a deep groove) on the anterior surface of the procingulum, but also penetrating deeply as an enamel fold; second primary fold present; second secondary fold absent; first minor fold present; anterolingual and anterolabial conulids usually not well differentiated from each other, and usually of nearly equal size; labial edge of anterolabial conulid does not extend to the anterior labial edge of the protoconid; protoconid nearly opposite the metaconid; hypoconid opposite or slightly behind entoconid.

M_2 procingulum obsolete or absent; first minor fold not evident; second primary fold usually well developed (rarely absent); posterolophid small to very small; anteroconulid absent, or rarely present as a small ridge or shelf.

M_3 subovate to subtriangular (with a rounded posterior apex) in outline from occlusal view; procingulum not evident; first minor fold not evident; first primary fold about midway on the tooth.

Baculum short or moderately long and tridigitate; the lateral digits longer and more robust than the medial digit; medial digit curved somewhat dorsad; baculum shorter than, to about as long as, the glans penis; basal sides of baculum concave dorsally and ventrally; baculum base more or less straight edged; distal end of baculum slightly enlarged and ball-shaped. Glans penis short and stubby to moderately long; exteriorly plain, with or without slight sulci dorsally and ventrally; bacular mounds smooth, and extending slightly above glans hood; hood variable in profile, being more or less straight, or sloped.

Karyotype, as far as known, consists of a diploid number of 60, with 116 autosomal arms; the X is a large submetacentric; the Y is a small submetacentric.

Comparisons.—Overall, *Andalgalomys* occupies a position intermediate to *Calomys* and *Eligmodontia* on the one hand, and *Graomys* on the other, being closer to the *Calomys-Eligmodontia* complex than to *Graomys*. In a linear arrangement, *Graomys* is somewhat intermediate between *Andalgalomys* and *Phyllotis* (*sensu stricto*). Externally, *Andalgalomys* is very similar to *Eligmodontia* in size, form, and coloration. It can be distinguished from *Eligmodontia* by its longer, more pencilled tail and its naked-soled, cushionless feet. Cranially, *Andalgalomys* differs from *Eligmodontia* by its somewhat larger skull; more wedge-shaped (less rounded) and ledged interorbital region; and its large palatine slits. Dentally, *Andalgalomys* differs from *Eligmodontia* in having upper molar cusps that are more ovate (less triangular) in outline. The M^1 of *Andalgalomys* has a well-developed anterior median fold (as opposed to shallow or obsolete fold); the anteromedian style is usually present on the procingulum of *Andalgalomys*, but is absent in *Eligmodontia*; the postcingulum of *Andalgalomys* is notched but is unnotched in *Eligmodontia*. The anteroloph of M^2 is directed anteriorly in *Andalgalomys* and anterolabially in *Eligmodontia*. The paracone and protocone of M^3 is divided from the hypocone and metacone by a deep major fold in *Andalgalomys*, but *Eligmodontia* has only a shallow major fold that does not bisect the tooth; the size of the tooth is smaller in *Eligmodontia*, and it is more square in outline (*Andalgalomys* is triangular in outline). The procingulum of M_2 is evident as an anteroconulid in *Eligmodontia*, but is absent or obsolete in *Andalgalomys*; the posterolophid is better developed (larger) in *Eligmodontia*. The first primary fold of M_3 is far anterior on the side of the tooth in *Eligmodontia*, but is located about midway on the tooth in *Andalgalomys*.

Andalgalomys is most similar cranially to *Calomys* (that is, *C. callosus* and *C. muriculus*, to which the following comparisons directly apply). Externally, *Andalgalomys* is somewhat larger than *Calomys*, with a noticably longer tail, and with large, non-volelike appendages. The ears are especially larger and broader. The skull of *Andalgalomys* differs from *Calomys* in having a more slender rostrum, including narrower nasals; the infraorbital foramen is larger in dorsal view; the bullae are much larger, and globular rather than tapered in shape; the upper toothrows are parallel sided rather than slightly divergent anteriorly; the incisive foramina are narrower; the mesopterygoid fossa is narrower. Dentally, *Andalgalomys* and *Calomys* are most similar. *Andalgalomys* differs from *Calomys* in having an anteromedian style on the procingulum of M^1, and a notch or fold on the postcingulum. The anteroloph of M^2 is directed anterolabially in *Calomys*, but anteriorly in *Andalgalomys*. The major fold of M^3 is shallow in *Calomys*, and unlike *Andalgalomys*, it does not bisect the tooth transversely by a complete enamel fold. The anterior median fold of M_1 is obsolete in *Calomys*, but well developed in *Andalgalomys*; unlike *Andalgalomys*, there is no notch on the postcingulum of *Calomys*; and the procingulum continues as a definite ridge onto the protoconid in Calomys. The procingulum of M_2 is not apparent in *Andalgalomys*, but is evident in *Calomys*.

Externally, *Andalgalomys* (especially *A. olrogi*) looks like a small *Graomys griseoflavus*. Compared to *Graomys*, the skull of *Andalgalomys* is smaller (but see remarks concerning *G. edithae*), with more wing-shaped (less triangular) interparietals; the palatines of *Graomys* are without slits; the parapterygoid fossa of *Andalgalomys* is relatively deeper and has a shelf on the anterior and medial borders. The upper molars of *Andalgalomys* are more brachydont, with more crested (not planed) occlusal surfaces; the cusps of *Andalgalomys* are more ovate (less triangulate), and are not as strongly laminated as in *Graomys*.

The procingulum of M^1 in *Graomys* is usually without an anterior fold (there may be a slight fold visible in unworn teeth), and has no anteromedial style. The anteroloph of M^2 is larger and directed more anterolabially in *Graomys*; the metacone and paracone are smaller than or equal to the hypocone and protocone in size in *Graomys*, but are larger than the hypocone and protocone in *Andalgalomys*. The anteroloph of M^3 usually is absent in *Andalgalomys*, but is present in *Graomys* (although of tiny size). The anterior median fold of M_1 is not apparent in *Graomys*; the labial edge of the anterolabial conulid extends to the anterolabial edge of the metaconid in *Graomys*, but does not approach the metaconid or protoconid in *Andalgalomys*; the protoconid is located much more posterior to the metaconid in *Graomys* than in *Andalgalomys*. The first minor fold of M_2 is present and moderately developed in *Graomys*, but is absent (or rarely obsolete) in *Andalgalomys*; the anteroconulid is present as a ridge in *Graomys*, but is absent or rarely represented by an obsolete ridge in *Andalgalomys*. M_3 of *Graomys* is strongly S-shaped and somewhat rectangular in outline, but is subtriangular and not S-shaped in *Andalgalomys*.

Andalgalomys is smaller than any of the *Phyllotis* species that approach its geographic range. It can be distinguished from most *Phyllotis* by its wedge-shaped (rather than rounded) interorbital region, its relatively longer rostrum, and its larger bullae. *Andalgalomys* is similar in size to *P. gerbillus*, but differs in its dental cusp patterns, in the features elaborated above, and in other details (Hershkovitz, 1962).

Remarks.—Graomys edithae Thomas is somewhat similar to *Andalgalomys olrogi*. Cabrera (1961) listed *edithae* in the synonomy of *G. griseoflavus medius* without comment. Our examination of the *G. edithae* holotype was made at a time when only one specimen of *A. olrogi* was available for direct comparison. That examination, and photographs of the skull and teeth of *edithae* in hand, lead us to the conclusion that *G. edithae* is not congeneric with *Andalgalomys*, nor conspecific with *G. griseoflavus*. Unfortunately, the molars of *edithae* are too worn to be of much use in making any specific determination.

Graomys hypogaeus Cabrera, from Corral Quemado, Catamarca, Argentina, is another named form that approaches the range of *Andalgalomys olrogi*, and which, from its description (Cabrera, 1934), appears to be similar in size and form to *Andalgalomys*. Cabrera later (1961) synonomized *G. hypogaeus* with *G. g. medius*. A cursory examination of the holotype convinced one of us (Mares) that *hypogaeus* is an old, and rather large *Eligmodontia typus*. We have been unable to measure or thoroughly examine the holotype, but photographs at hand, kindly provided by E. Massoia, and an analysis of Cabrera's measurements (1934) reconfirm our conclusions that *G. hypogaeus* is an *Eligmodontia typus* (see discussion).

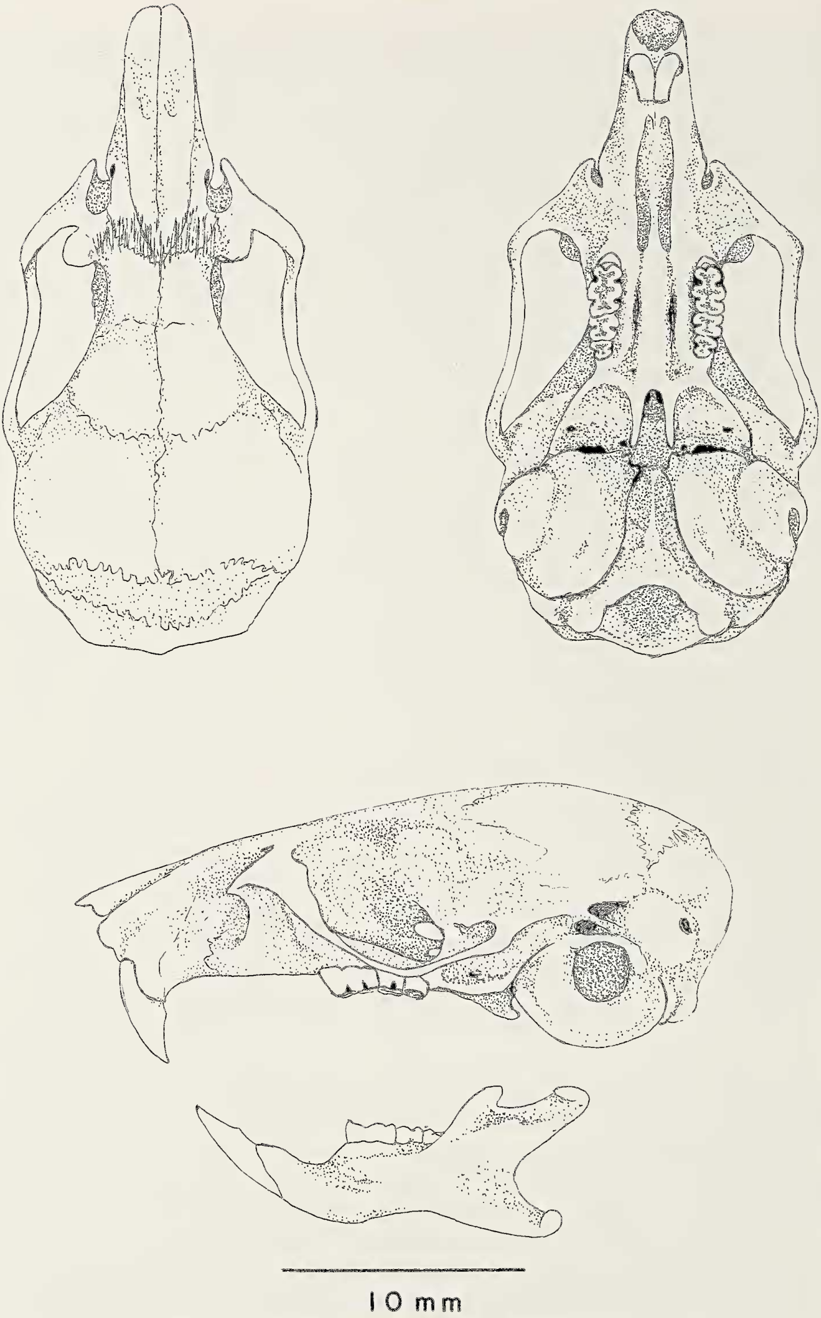

Fig. 1.—Skull of *Andalgalomys olrogi* holotype (CM 44024).

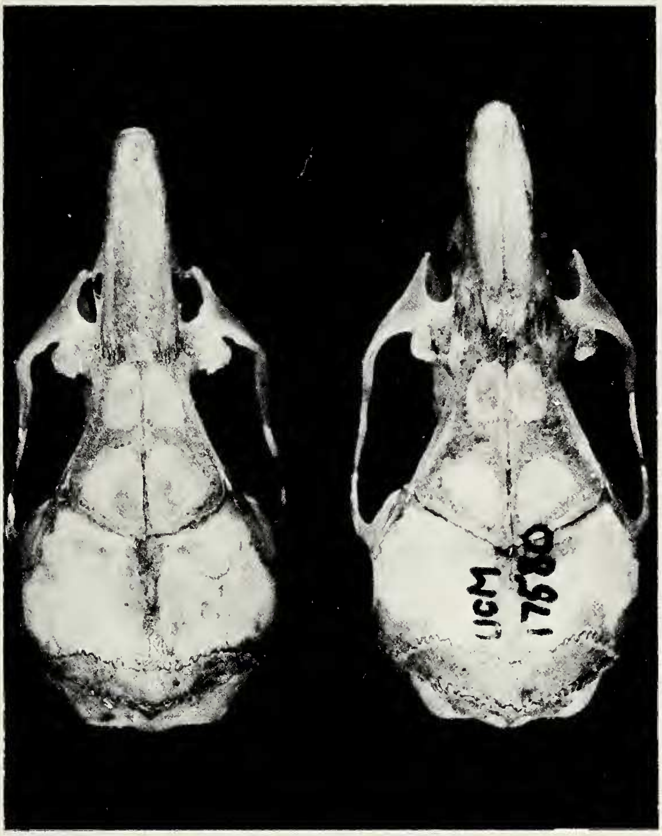

Fig. 2.—Dorsal view of skulls of mature specimens of *Andalgalomys*. Left, *A. olrogi* (CM 44023); right, *A. pearsoni* (UCONN 17580).

Andalgalomys olrogi, new species

Holotype.—Young adult female; skin, skull, and chromosomes, CM 44024; from West Bank Rio Amanao, about 15 km W (by road) Andalgalá, Catamarca Province, Argentina; obtained 19 January 1976 by D. F. Williams, original No. 2077.

Distribution.—Known only from three localities in the vicinity of the Rio Amanao, westward from Andalgalá in central Catamarca. Approximate elevation at the three localities is 950 m.

Diagnosis.—A moderately small, yellowish-brown mouse with a small whitish subauricular spot and a small, whitish postauricular patch; tail relatively long and moderately pencilled; pinnae large and

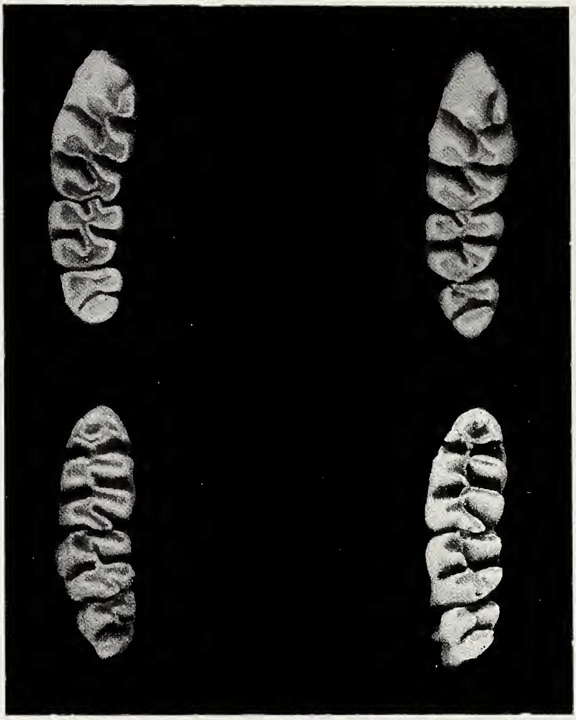

Fig. 3.—Upper and lower molar rows of *Andalgalomys*. Left, *A. olrogi* holotype (CM 44024); right, *A. pearsoni* (UCONN 17566). The molars of *A. olrogi* are slightly more worn than those of *A. pearsoni*. The teeth are coated with a layer of ammonium-chloride dust in order to reduce glare and to highlight the cusps and enamel folds.

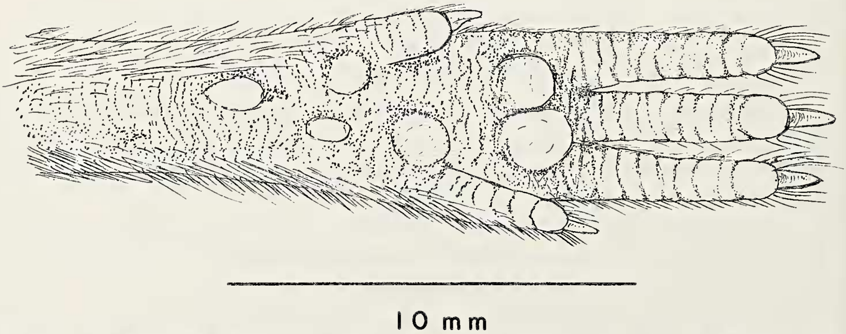

Fig. 4.—Left hind foot of *A. olrogi*. The drawing is a composite, based largely upon photographs of fresh material.

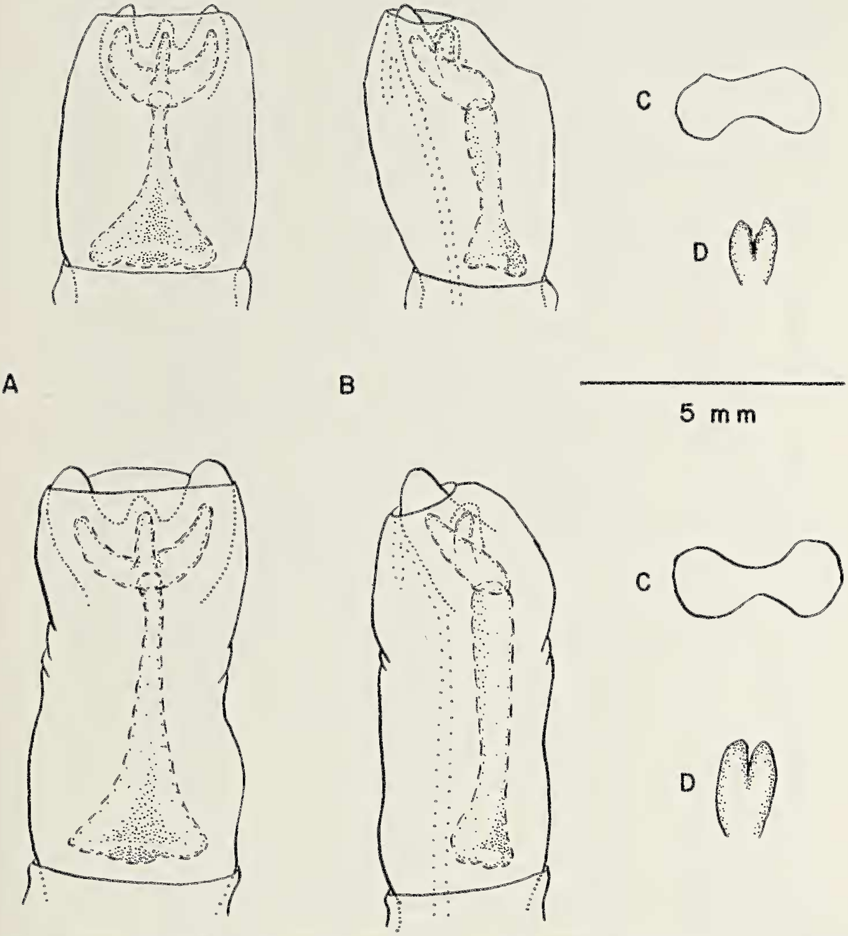

Fig. 5.—Phalli of *Andalgalomys*. Upper, *A. olrogi*; lower, *A. pearsoni*. A = ventral view; B = lateral view; C = outline of base of the baculum, its dorsal surface facing up; D = ventral view of urethral flaps. The drawings are composites.

broad; hairs on ventral body surfaces and upper surfaces of the feet white to their bases; pelage moderately long (hairs average about 10 mm on rump) and lax. Skull with wedge-shaped interorbital region; palatines with long slits in place of separate foramina; interparietal bones narrow, more or less wing-shaped in outline.

Etymology.—This species is respectfully and affectionately named in honor of Dr. Cläes Christian Olrog, who has made so many outstanding contributions to the knowledge of South America's fauna.

Table 1.—*External and cranial measurements for* Andalgalomys, Calomys, Eligmodontia, *and* Graomys. ^{a} = P ≤ *0.05;* ^{b} = P = *0.01. The significance values refer to the differences between* A. olrogi *and* A. pearsoni.

Character	*Andalgalomys olrogi*							*Andalgalomys pearsoni*												
	44020	44021	44022	44023	44024	M	SE	17562	17563	17566	17568*	17575*	17579	17580	M	SE	*Calomys callosus* M	*Calomys muriculus* M	*Eligmodontia typus* M	*Graomys griseoflavus* M
N						5									5	5	5	5	5	5
Tail length	126	125	130	127	127	127^{b}	0.84	117	105	110	113	92	97	111	108	3.35	80	73	104	158
Head-body length	86	113	106	108	91	100	5.21	98	95	90	91	103	89	115	97	4.70	92	98	76	121
Hind foot length	23.9	24.7	24.6	24.9	23.8	24.4	0.22	24.0	23.0	25.0	24.0	24.0	22.0	24.0	23.6	0.51	23.3	20.0	23.4	28.5
Ear length	22.0	19.6	20.2	21.1	20.0	20.6^{a}	0.43	20.0	19.0	18.0	19.0	19.0	19.0	20.0	19.2	0.37	20.3	16.5	19.3	26.9
Greatest skull length	27.7	28.4	30.0	29.9	27.1	28.6	0.58	30.2	29.5	27.8	28.6	25.6	28.1	30.8	29.3	0.58	26.2	26.2	24.3	31.8
Condylobasal length	25.0	25.7	27.5	26.9	24.2	25.9	0.60	27.5	26.4	24.6	26.5	23.5	25.6	27.8	26.4	0.59	24.4	24.0	22.1	29.5
Zygomatic breadth	13.5	14.0	14.5	14.1	13.3	13.9	0.22	14.6	14.7	12.9	14.5	13.4	13.8	14.8	14.2	0.36	14.3	14.0	12.6	16.0
Braincase width	12.5	13.0	12.8	12.9	12.3	12.7	0.12	13.0	13.2	12.5	13.3	11.4	12.4	12.8	12.8	0.15	11.7	11.3	11.7	13.8
Least interorbital breadth	4.5	4.6	4.7	4.8	4.4	4.6^{a}	0.07	5.2	4.8	4.7	4.9	4.2	4.8	5.1	4.9	0.10	4.3	4.5	4.2	5.1
Interparietal length	1.5	1.9	2.0	2.2	1.9	1.9^{b}	0.11	3.6	3.5	2.6	3.1	2.7	2.5	3.1	3.1	0.23	2.4	3.0	2.2	3.5
Nasal length	11.3	11.4	12.1	12.5	11.1	11.7	0.27	12.0	11.7	10.4	11.1	10.2	11.6	12.2	11.6	0.31	10.7	10.5	9.3	12.9
Nasal width	2.5	2.4	3.0	2.8	2.5	2.6	0.11	3.0	2.9	2.6	2.5	3.0	2.6	3.0	2.8	0.09	2.9	3.1	2.6	3.6
Rostral width	4.0	4.5	4.4	4.0	3.8	4.1^{a}	0.13	5.2	5.0	4.4	4.8	4.8	4.5	5.8	5.0	0.25	4.6	4.7	4.1	5.2
Palatilar length	12.4	13.2	13.2	12.1	12.4	12.7	0.22	13.4	13.0	12.1	13.0	10.8	12.4	14.4	13.1	0.39	11.3	10.8	10.4	13.6
Incisive foramen length	5.5	6.7	6.4	5.7	6.0	6.1	0.22	6.3	6.1	5.8	6.1	6.3	6.0	6.8	6.2	0.17	5.6	6.0	5.2	7.3
Diastema length	7.5	7.5	7.7	7.0	7.1	7.4	0.13	8.1	7.6	6.9	7.6	6.1	7.1	8.3	7.6	0.27	6.3	6.3	5.8	8.0
Maxillary toothrow length	4.1	5.0	4.5	4.5	4.7	4.6	0.15	4.9	4.8	4.9	4.9	4.6	4.7	4.9	4.8	0.04	4.5	4.2	4.0	5.5
Distance between molar rows	3.1	3.0	3.3	2.9	3.0	3.1	0.07	2.9	3.0	3.6	3.0	2.6	2.8	3.2	3.1	0.14	2.8	2.8	2.6	2.9
Distance across molar rows	5.9	6.1	6.0	5.7	5.8	5.9	0.07	6.0	6.0	5.2	6.0	5.1	5.7	6.4	5.9	0.20	5.5	5.3	5.0	6.2
Parapterygoid fossa width	1.8	1.9	2.0	1.7	1.8	1.8	0.05	1.8	1.8	1.6	1.8	1.4	1.7	1.8	1.7	0.04	1.8	1.4	1.6	1.6
Mesopterygoid fossa width	0.5	0.5	0.6	0.7	0.7	0.6	0.05	0.4	1.0	1.0	1.0	0.9	0.8	0.8	0.8	0.11	1.0	1.1	0.7	1.2
Bullar length	6.5	7.0	6.5	6.0	6.4	6.5^{b}	0.16	5.5	5.4	5.3	5.2	4.2	5.4	5.4	5.4	0.03	3.9	4.0	5.1	6.8

Table 1.—(*Continued*)

Character	*Andalgalomys olrogi*							*Andalgalomys pearsoni*									*Calomys callosus* M	*Calomys muriculus* M	*Eligmodontia typus* M	*Graomys griseoflavus* M
	44020	44021	44022	44023	44024	M	SE	17562	17563	17566	17568*	17575*	17579	17580	M	SE				
No. palatine foramina, right	2	2	2	2	2	2	0.00	2	3	2	3	4	5	2	2.8	0.58	4	4	4	4
No. palatine foramina left	2	2	2	2	2	2[a]	0.00	2	4	3	3	2	4	3	3.2	0.37	4	5	4	4
Incisive foramina intrusion	0.2	0.4	0.1	0.1	0.1	0.2	0.06	0.2	0.3	0.4	0.2	0.7	0.2	0.4	0.3	0.05	0.7	0.8	0.4	0.7
M^1 length	2.1	2.0	1.9	2.0	2.0	2.0	0.03	2.1	2.0	2.1	2.0	1.9	2.0	2.2	2.1	0.04	1.8	1.7	1.7	2.1
M^2 length	1.0	1.1	1.0	1.0	1.1	1.0	0.02	1.1	1.0	1.0	1.1	1.1	1.0	1.1	1.0	0.02	1.1	1.1	1.0	1.3
M^3 length	0.9	0.9	0.9	0.8	0.9	0.9	0.02	0.8	0.9	0.9	1.1	0.8	0.8	0.9	0.9	0.02	0.8	0.9	0.6	1.1
M^1 width	1.4	1.3	1.3	1.3	1.3	1.3	0.02	1.3	1.5	1.5	1.4	1.2	1.5	1.5	1.5	0.04	1.2	1.1	1.0	1.5
M^2 width	1.1	1.2	1.1	1.2	1.2	1.2	0.02	1.0	1.2	1.2	1.2	1.1	1.2	1.4	1.2	0.06	1.1	1.0	0.9	1.3
M^3 width	1.0	1.0	0.9	1.0	1.0	1.0	0.02	0.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.02	0.9	0.9	0.7	1.1
Mandibular toothrow length	4.1	4.1	4.1	4.1	4.4	4.2[a]	0.06	4.5	4.5	4.5	4.5	4.3	4.2	4.5	4.5	0.07	4.3	4.0	3.9	5.1
M_1 length	2.0	1.9	1.9	1.9	1.9	1.9[b]	0.02	2.0	2.0	2.0	2.1	1.6	2.0	2.1	2.0	0.02	1.6	1.5	1.5	2.0
M_2 length	1.0	1.1	1.0	1.1	1.1	1.1	0.02	1.1	1.1	1.1	1.1	1.1	1.1	1.0	1.1	0.02	1.1	1.1	1.0	1.3
M_3 length	0.9	1.0	0.8	0.8	0.9	0.9	0.04	0.8	0.8	0.9	0.9	1.0	0.8	0.8	0.8	0.02	1.1	1.0	0.8	1.1
M_1 width	1.2	1.3	1.2	1.2	1.3	1.2[a]	0.02	1.3	1.4	1.3	1.4	1.1	1.3	1.4	1.3	0.02	1.1	1.1	1.0	1.4
M_2 width	1.2	1.3	1.2	1.1	1.3	1.2	0.04	1.3	1.3	1.2	1.3	1.1	1.2	1.3	1.3	0.02	1.1	1.1	0.9	1.3
M_3 width	0.9	1.1	0.9	0.9	1.0	1.0	0.04	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.00	0.9	0.9	0.7	1.1

* Immature, not used in statistical anaylses.

Fig. 6.—Karyotype of *A. olrogi* male (CM 44022), from west bank Rio Amanao, about 15 km W (on Route 62) Andalgalá, Catamarca Province, Argentina.

Description.—External, cranial, and phallus measurements are presented in Tables 1 and 2. Characters are as described for the genus, elaborated below, and depicted in Figs. 1–5. Dorsal coloration is closest to Light Ochraceous Buff (capitalized terms from Ridgway, 1912), overlain with a light suffusion of black-tipped hairs, except on the sides, which are buffy, and on the face, which has a mixture of buffy and white hairs; regions around external nares, the dorsal-medial and posterior bases of the pinnae, and a spot below the pinnae are pure white; tops of feet and ventral parts, including the underside of the tail are white, the hairs being white to the base. Tail brownish above, moderately haired, slightly crested (hairs increasing in length on the dorsal surface toward the tip), and moderately pencilled (hairs extending about 5–9 mm beyond tip). Ears large, broad, and sparsely haired with fine, brownish hairs. Soles of feet naked, with six moderately large plantar tubercles (Fig. 4); plantar surfaces finely scutellate, and unpigmented (not blackish); first hind digit very short, not reaching the base of digits 2 to 4; tarsal elements of digits 2 to 4 somewhat elongated.

Table 2.—*Baculum and glans penis measurements of* Andalgalomys.

Species	Catalog no.	Glans		Baculum lengths			
		Length	Diameter	Total	Proximal bone	Medial digit	Lateral digit
A. olrogi	44020* CM	3.5	2.2	3.5	2.5	1.1	1.1
A. olrogi	44022 CM	—	—	4.4	3.0	1.2	1.4
A. olrogi	44023 CM	—	—	4.3	3.0	1.4	1.5
A. pearsoni	17568* UCONN	6.3	2.8	5.5	4.4	1.1	1.8
A. pearsoni	17575* UCONN	6.2	3.0	5.5	4.1	1.3	1.6
A. pearsoni	17580 UCONN	7.4	3.1	6.3	5.0	1.3	1.7

* Immature, baculum not fully ossified.

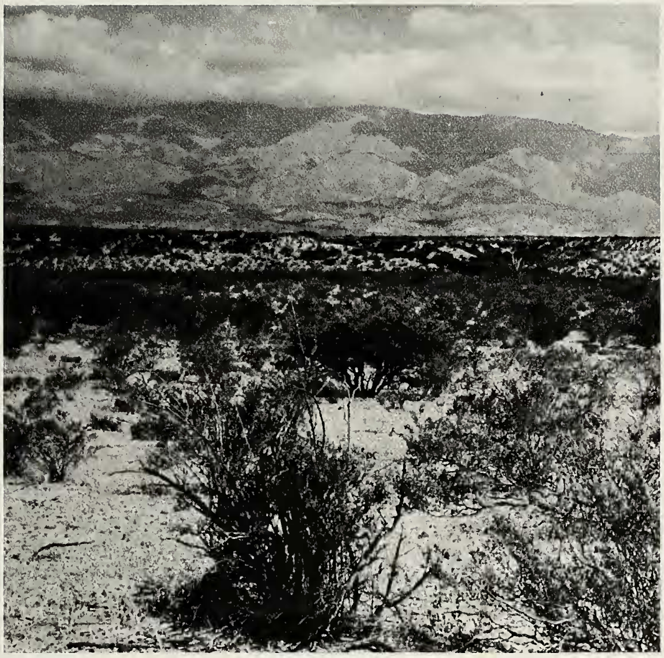

Fig. 7.—Creosote bush (*Larrea cuneifolia*) flat with associated mixed shrubs (*Acacia* and *Bulnesia*) and saguaro-like cacti (*Trichocereus*) in the background, west of Andalgalá, Catamarca Province, Argentina.

Bullae large; interparietal broad and narrow (in anterior-posterior aspect) in appearance (Figs. 1 and 2). Anteromedian style on anterior surface of M^1 well developed; mesostyle tiny, but apparent; anteroconule small, but evident; anterolabial style present and well developed, but not apparent in worn teeth (Fig. 3).

Phallus short and stubby; baculum about the same length as glans penis length (Table 2); baculum relatively robust; glans hood angled back sharply, being longer on the ventral surface than the dorsal surface (Fig. 5).

The karyotype is presented in Fig. 6. The diploid number is 60, and the number of autosomal arms is 116 (total arms number = 120); the X-chromosome is a large submetacentric and the Y-chromosome is a small submetacentric.

Comparisons.—*A. olrogi* differs from *A. pearsoni* in being lighter colored (lighter yellowish-brown and with less of a blackish overwash); in having relatively larger, broader pinnae; in its longer, laxer pelage; and in having a more hirsute and pencilled tail of longer length. Cranially, its bullae are more inflated and of longer length, its zygomatic arches are more robust, and its interparietals are shorter. The well-developed anteromedian style, the presence of a mesostyle, and the occurrence of a small anteroconule on M^1 are dental features that differ from *A. pearsoni*. The phallus of *A. olrogi* is shorter and stubbier than that of *A. pearsoni* (Table 2 and Fig. 5), and has a unique dorsally-sloping hood.

A. olrogi is distinguishable from *E. typus* externally by its lack of hairy cushions on the hind feet and its longer tail. For other remarks concerning ways that *Andalgalomys* and *Eligmodontia* differ, see the generic description. *Calomys callosus* can be distinguished by its more volelike external appearance (that is, its small appendages, especially its shorter ears and shorter, non-pencilled tail).

Habitat and associates.—All five specimens were trapped in or near *Larrea* (creosote brush) stands, on fine-textured soils on the floor of the Bolsón de Pipanaco (Fig. 7). Trapping by Mares periodically over a six-year period in the same area, as well as south in Mendoza Province and northward through the provinces of Tucumán and Salta, has failed to produce any other specimens. *G. griseoflavus* is fairly common in the same area, but is generally captured only in *Prosopis* and *Acacia* trees along the arroyos or on rocky upper bajadas (Mares, 1976). *E. typus* and *C. musculinus* were the only other cricetines trapped in the same habitat. *E. typus* is common on the creosote-flats. *C. musculinus* is very rare in this habitat (being more common in riverine habitats, Mares, 1977c), and was captured only a single time in the same area as *A. olrogi*.

Remarks.—The holotype is somewhat immature and some skull characters are not fully developed (especially the supraorbital ledges). However, the dental cusps are largely unworn, and portray well the cusp patterns that are diagnostic for this species.

Specimens examined.—ARGENTINA. *Catamarca*: along Rio Amanao, about 13 km S, 15 km W Andalgalá, 1 ♂, skin, skull, phallus, and body in fluid (CM 44020); 10 km W Andalgalá (by road on Route 62, at km marker 10), 1 ♀, skin, skull, and chromosomes (CM 44021); West Bank Rio Amanao, about 15 km W (on Route 62) Andalgalá, holotype, plus 2 ♂, skins, skulls, phalli, and chromosomes (CM 44022, 44023).

Andalgalomys pearsoni (Myers)

Graomys pearsoni Myers, Occas. Pap. Mus. Zool., Univ. Michigan, 676:1, 18 March 1977.

Holotype.—Adult male; skin and skull, MVZ 145276; from 410 km NW Villa Hayes by road, Departamento Boquerón, Paraguay obtained 24 September 1973 by P. Myers, original No. 1161 PM.

Distribution.—Known from 0.5 km S Teniente Enciso, and 2.5 km S Teniente Enciso (km 655 Trans Chaco), Departamento Nueva Asunción, Paraguay; and from the type locality (Myers, 1977).

Diagnosis.—A moderately small, yellowish-brown mouse with a grayish overwash of black-tipped hairs; tail brownish, longer than head-body length, and sparsely haired (pencil <3 mm). Hairs on ventral surfaces and on feet white to their bases; pelage not noticeably long or lax. Skull with wedge-shaped interorbital region; palatines with or without long slits; interparietals of short length and more or less wing-shaped in outline. Phallus relatively long, with moderately large and robust baculum.

Description.—External, cranial, and phallic measurements of five adult and two immature paratypes are presented in Tables 1 and 2. Characters are as described for the genus, elaborated below, and illustrated in Figs. 2, 3, and 5. Refer to Myers (1977) for additional illustrations and measurements. Color closest to Ochraceous-Tawny (Ridgway, 1912), overlain with a moderate to heavy suffusion of black-tipped hairs; tops of feet and ventral parts with hairs white to their bases; small white subauricular spot; face brownish, not noticeably lighter than dorsal parts of body (but without heavy suffusion of black); tail bicolored, brownish above and buffy-white below. Pelage of normal length (hairs on rump averaging about 7 mm). Tail of moderate length, sparsely haired, and with a very slight pencil (hairs <3 mm beyond tip). Ears of moderate size, not noticeably broadened, sparsely haired, and brownish in color. Soles of feet naked, with six medium-sized plantar tubercles; plantar surfaces coarsely scutellate, and darkly pigmented; first hind digit short; digits 2 to 4 not noticeably elongated relative to digit 5.

Bullae moderately inflated; interparietals of moderate length and somewhat wing-shaped. Anteromedian style on the anterior surface of M^1 obsolete (tiny or not visible); mesostyle absent; anterolabial style absent or rarely represented by a small shelf or style; anteroconule absent (Fig. 3).

Phallus relatively long, with the glans hood angled slightly ventrad (Fig. 5); baculum shorter than glans length, but relatively long and not noticeably delicate (Table 2).

Comparisons.—Refer to the account of *A. olrogi* for a comparison with that species. *A. pearsoni* is larger and with a much longer tail than sympatric *Calomys*. Its general appearance is not vole-like or *Mus*-like, differing in this respect from *Calomys*. For other characters that are useful in distinguishing *Calomys* from *A. pearsoni*, see the preceding generic description. From *G. griseoflavus chacoensis*, *A. pearsoni* can be distinguished by its smaller size, proportionately smaller ears, and its shorter, non-pencilled tail. For other details, refer to the generic description.

Habitat.—According to Myers (1977), *A. pearsoni* inhabits dry grasslands, which occur as islands in the western Chaco of Paraguay.

Specimens examined.—PARAGUAY. *Nueva Asunción*: Teniente Enciso, 4 ♂, 1 ♀, skins, skulls, and 2 phalli (UCONN 17562, 17563, 17566, 17568, 17575); 0.5 km S Teniente Enciso, 1 ♂, 1 ♀, skins, skulls, and phallus (UCONN 17579, 17580).

RESULTS AND DISCUSSION

Measurements for 38 morphometric traits for both species of *Andalgalomys*, and for comparable samples of other related phyllotines, are given in Table 1. Ten of the 38 characters are significantly different ($P \leq 0.05$) in *A. olrogi* and *A. pearsoni*. Five of these differences are highly significant ($P \leq 0.01$), despite the small sample sizes. Particularly distinctive measurements include tail length, bullar length, and interparietal length, all of which will readily distinguish *A. olrogi* from *A. pearsoni*.

Table 3.—*Matrix of similarity for 51 dental characters. See the generic and species descriptions for the characters utilized. The values for species pairs indicate the number of shared characters between taxa. Unique traits indicates the number of traits not shared with other taxa.*

Species	*Andalgalomys pearsoni*	*Calomys callosus*	*Eligmodontia typus*	*Graomys griseoflavus*	Unique traits	
Andalgalomys olrogi	43	28	27	27	3	6
Andalgalomys pearsoni	—	39	29	29	0	
Calomys callosus	—	—	40	34	0	
Eligmodontia typus	—	—	—	31	3	
Graomys griseoflavus	—	—	—	—	6	

Bacular and glans penis data are listed in Table 2, and Fig. 5 illustrates the phalli of *Andalgalomys*. Unfortunately, we had no intact phalli from mature individuals of *A. olrogi* (but there are mature bacula); and two of the three phalli of *A. pearsoni* are immature with only partially ossified bacula. The mature bacula of *A. olrogi* are much shorter than *A. pearsoni*, but the two species are similar in relative size of the digits, in the general outline of the baculum, in the dorsal-ventral concavity of the basal bacular shafts, and in the ball-shaped distal end of the baculum. These similarities, especially the digit proportions (a smaller, more slender medial digit) and the dorsal inflection of the medial digit are a combination of characters unlike any illustrated by Hooper (1962) or Hooper and Musser (1964). The bacular shaft (osseous baculum) is similar to *Phyllotis osilae* and *P. magister* (Pearson, 1958), and *P. andinum*, *P. amicus*, and *P.* (*Auliscomys*) *pictus* (Hershkovitz, 1962). We know nothing of the cartilaginous digits in these taxa, however.

The shape of the glans penes of the *Andalgalomys* species appear to be divergent. How much of this is due to immaturity, how much is due to different preservation techniques of the glans available to us for study, and how much reflects real differences cannot be answered with certainty. *A. olrogi* is unique in its dorsally-canted hood. Otherwise, its glans penis resembles *C. callosus* (Hooper and Musser, 1964). The glans penis of *A. pearsoni* is not particularly similar to any of the phyllotines known to us, but is, perhaps, closer overall of *E. typus* than to others illustrated in Hooper and Musser (1964).

A numerical summary of the similarities in dental traits between *Andalgalomys*, *Calomys*, *Eligmodontia*, and *Graomys* is given in Table

3. These traits were evaluated qualitatively (for example, the presence or absence of a style, the shape of a tooth, the relative size of cusps, and the positions of folds). In tabulating similarities, subjective judgements were sometimes necessary, but we do feel that the numbers reflect the relative degree of similarity of the various genera to *Andalgalomys*. Note that *A. olrogi* and *A. pearsoni* share more traits (43) than either does with other genera, and that *A. pearsoni* is more similar to *Calomys* and to *Eligmodontia* (although all of the shared characters are not the same) than is *A. olrogi*. *A. pearsoni* is more variable than is *A. olrogi* (species with variable conditions for a trait were regarded as being similar to both those that possessed and those that lacked a trait). This is why *A. pearsoni* can share 39 traits with *Calomys*, whereas *A. olrogi* shares only 28. *Andalgalomys* is somewhat less similar to *Eligmodontia*, which has a different dental pattern. *Eligmodontia* has a somewhat hypsodont and relatively well-crested molar arcade. This could indicate some importance of insects in its diet, especially hard, chitinous species such as coleopterans. *Andalgalomys* is least similar to *Graomys*. *Graomys* has a relatively well-developed triangulate, planed, and hypsodont pattern that is familiar to many grazing and browsing species, including many of the more evolved phyllotines. *Andalgalomys* seems to be progressing towards a laminated and perhaps planed molar pattern.

Overall, we regard *Calomys* as the most primitive group of phyllotine species, and the ones closest phenetically to the oryzomyines. Primitive traits include their persistently brachydont, tuberculate dentition, their more classically "murine" skull (that is, a sharply ridged supraorbital region, relatively unconstricted interorbital region, and a robust rostrum), and their generally unspecialized appendages. The most divergent *Calomys* are somewhat akodonlike externally with the volelike suite of adaptations that most obviously includes shortened appendages and microtinelike pelage. Populations of *C. callosus* from Catamarca, Argentina, illustrate this condition well. However, these tendencies are not nearly as well developed in *Calomys* as they are in some other phyllotines (and in akodonts and sigmodonts in general). We do think that some *Oryzomys* (especially *Oligoryzomys*) are not too unlike *Calomys*, although their dental differences are certainly trenchant.

In its non-dental morphological features, *A. pearsoni* is more primitive and closer to *Calomys* than is *A. olrogi*. Its somewhat harsher pelage, smaller and narrower ears, shorter and less-specialized feet, shorter and less-pencilled tail, less-inflated bullae, and greater number of palatine foramina are notably primitive characters for *Andalgalomys*. Overall, though, the similarities between *A. pearsoni* and *A. olrogi* are much greater than their differences. This is especially well

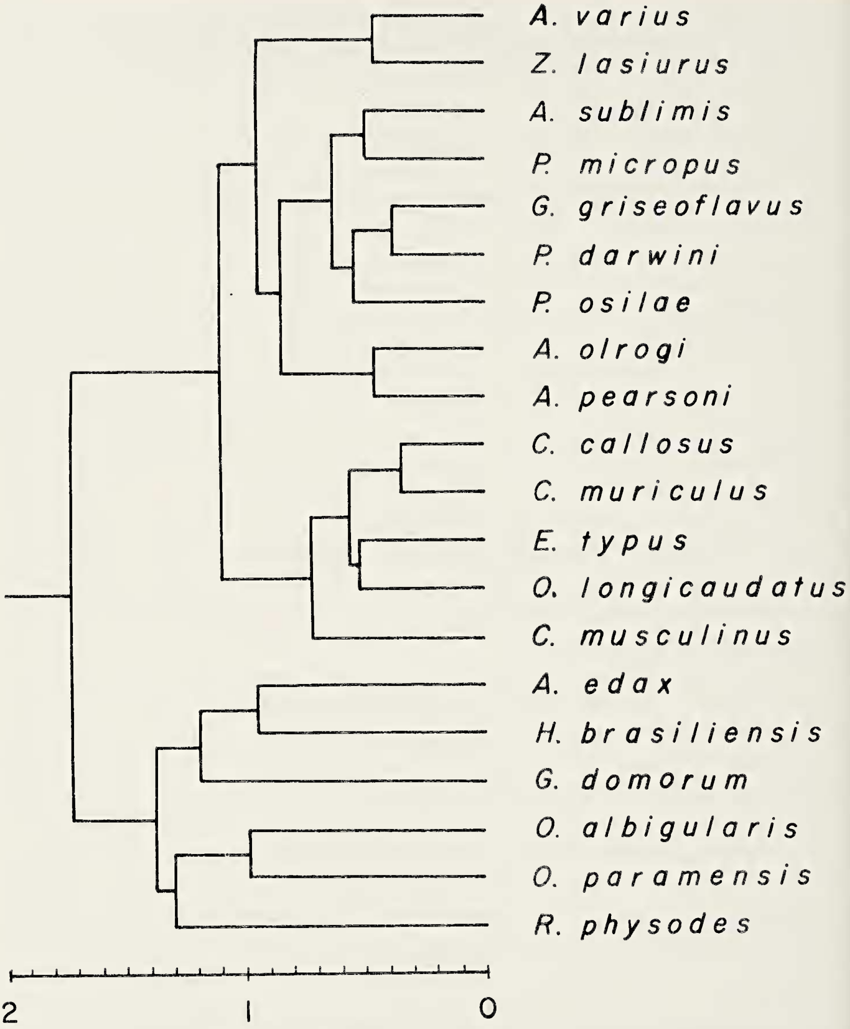

Fig. 8.—Phenogram, based upon taxonomic distance, of several South American cricetine species. The cophenetic correlation coefficient is 0.73.

illustrated by the results of the multivariate analyses of the morphometric traits.

The results of the numerical analysis based upon average Euclidean distance are shown in Fig. 8. Taxa with the lowest distance values are closest together in 38 dimensional space. The holotypes of *G. edithae* and *G. hypogaeus* were not included because we had no measurements

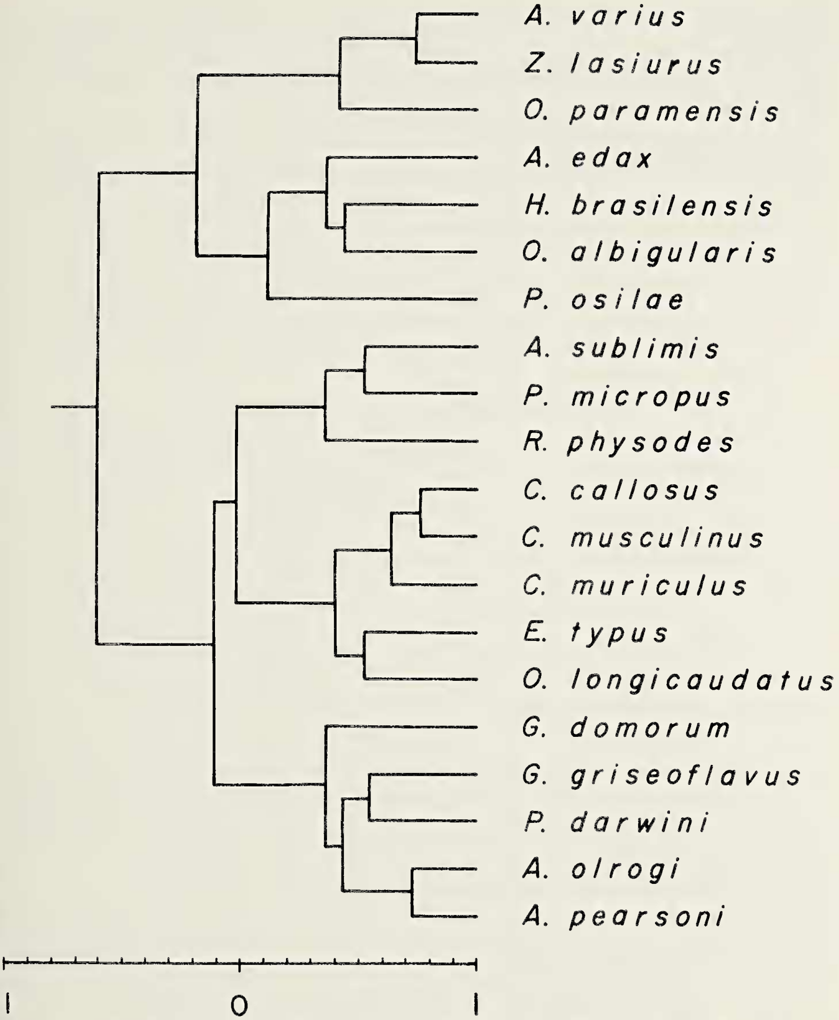

Fig. 9.—Phenogram, based upon Q-mode correlation coefficients, of several South American cricetine species. The cophenetic correlation coefficient is 0.78.

for several characters for these individuals. Note that *A. olrogi* and *A. pearsoni* are most similar to each other (distance = 0.47), and that *Andalgalomys* is most closely linked with a cluster that includes *Auliscomys*, *Phyllotis*, and *Graomys* (Fig. 8). *Akodon* and *Zygodontomys* are united with the above taxa, but are about equally similar phenetically (average taxonomic distance) to the cluster that includes *Calo-*

mys, *Eligmodontia*, and *Oryzomys longicaudatus*. Several relatively specialized, and generally dissimilar taxa, including *Andinomys*, *Holochilus*, *Oxymycteris*, *Oryzomys albigularis*, and *Reithrodon* are linked with a large *Graomys* (*G. domorum lockwoodi*).

A summary of the numerical analysis using Q-mode correlation coefficients is presented in Fig. 9. Taxa that are most similar in proportions will exhibit the highest positive similarity coefficients. *A. olrogi* and *A. pearsoni* are more similar ($r = 0.73$) to each other than are any other pair of taxa except for *Akodon* and *Zygodontomys* ($r = 0.74$). *Andalgalomys* is most similar, proportionately, to *P. darwini* and *G. griseoflavus* (Fig. 9). These taxa, in turn, are clustered with a group that includes *Calomys*, *Eligmodontia*, *O. longicaudatus*, *Auliscomys*, *P. micropus*, and *Reithrodon*.

The distance and similarity phenograms both show a strong phenetic relationship between *A. olrogi* and *A. pearsoni*. *Eligmodontia* is linked most closely with *O. longicaudatus* in both analyses, but is most similar phenetically to *Calomys*, among the phyllotines. Neither phenogram (Figs. 8 and 9) portrays precisely the relationships that we perceive subjectively from our examination of dental cusp patterns (Table 3) and of the karyotypic variation of phyllotines (Fig. 10). The phenograms are fairly accurate summaries of the morphological similarities (excluding dental cusp-patterns) of these taxa, although all of the intertaxa relationships cannot be shown in the phenograms. The cophenetic correlation coefficients are not particularly high (0.78 for the similarity phenogram and 0.73 for the distance phenogram), indicating that considerable information is lost in the summaries. Furthermore, it should be stressed that the numerical methods utilized are measures of phenetic similarities. They do not distinguish between similarities due to parallelism, convergence, and common ancestry.

A discriminant analysis, utilizing measurements of *G. hypogaeus* (Cabrera, 1934) and *G. edithae* (Thomas, 1919) was performed in order to provide a quantitative assessment of their phenetic similarities to other taxa, and in order to attempt to classify them with one or more of these taxa. The characters used were the 13 measurements common to the two reports. The potential groups into which these forms could be classified by the analysis included *A. olrogi*, *A. pearsoni*, *C. callosus*, *E. typus*, and *G. griseoflavus*. Both *G. edithae* and *G. hypogaeus* were closest to *E. typus* in this analysis, with D^2 values of 45.3 and 92.9, respectively (the mean intragroup D^2 for *E. typus* was 11.3). These data should be interpreted with caution, as the characters utilized are not very diagnostic, and external dimensions and size have a heavy influence in these statistics. Our examination of the *G. edithae* holotype revealed several characters that are clearly not associated with *Eligmodontia*, but are representative of *Graomys*. Most notable

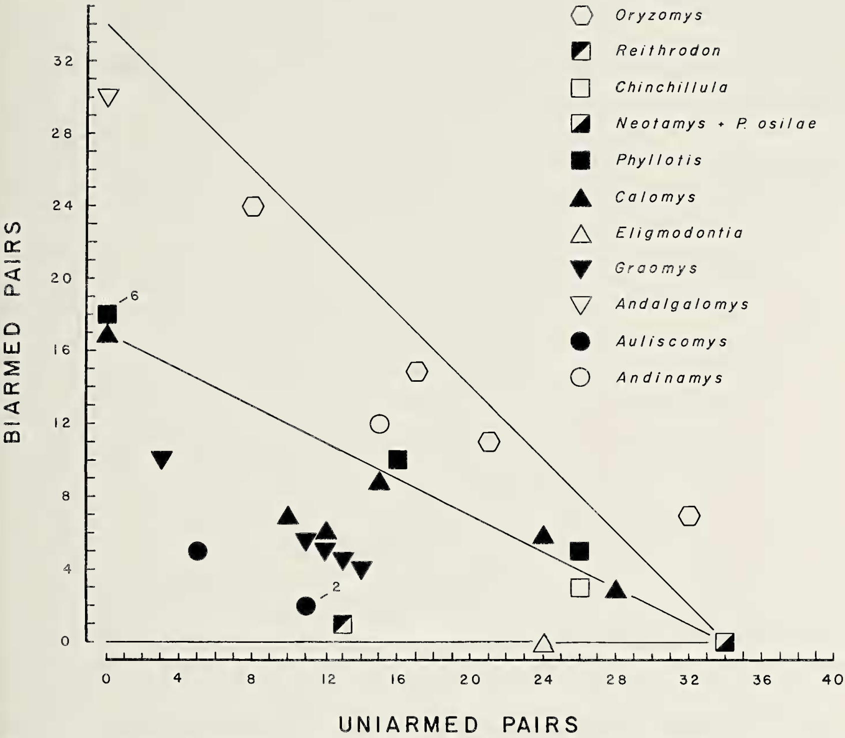

Fig. 10.—Autosomal karyotypic variation of phyllotine rodents and of *Oryzomys albigularis*. Arm additions (pericentric inversions or other addition processes) that result in changes in FN cause displacement along a line whose angle is depicted in the uppermost line. Robertsonian processes (changes in 2*n*) result in numerical changes along the angle shown in the middle line. Tandem fusions (changes in 2*n* and FN) cause displacement to the left along a horizontal line such as the bottom line. The numbers indicate the number of species sharing the same karyotype, whereas unnumbered symbols indicate the karyotypes of single species. The data are from Pearson and Patton (1976), Gardner and Patton (1976), and unpublished data.

in this regard are the narrow procingulum of M^1 in *G. edithae*, which is deeply divided from the protocone-metacone by deep anterior median and lingual folds, and the deep major fold on the M^3 of *G. edithae*. The paratypes of *G. edithae* (from near Chumbicha, Catamarca, at an elevation nearly 2,000 m lower than the type locality), represent, in our opinion, *G. griseoflavus medius*. The skull of *G. hypogaeus*, as we know it from a cursory examination and from photographs, is clearly an *E. typus*. However, one of us (Williams) considers it probable that the skin of *G. hypogaeus* is not *E. typus*. This is so, because Cabrera

(1934) explicitly compares *G. hypogaeus* to *E. typus* and remarks upon the naked soles of *G. hypogaeus*, and because the tail is proportionately longer (142% of head-body length) than is typical of *E. typus*. Also, the tail has a well-developed pencil (about 10 mm in length) and the ear pinnae are larger than those of *E. typus* from the same general region. Whether or not the *G. hypogaeus* holotype is a composite of an *E. typus* skull and the skin of some other species cannot be resolved until the specimen can be carefully examined.

Karyotypically, *A. olrogi* is the most divergent of the phyllotines so far examined (Figs. 6 and 10). Its relatively high diploid number and all-biarmed complement makes it unusual among the Sigmodontini (see Gardner and Patton, 1976). The only species similar to *A. olrogi* is *Oryzomys albigularis* from Colombia. Comparison of the karyotype of *A. olrogi* with the figure of *O. albigularis* from Gardner and Patton (1976) suggests a striking similarity. Three centric fusions and the pericentric inversion of two acrocentric pairs of autosomes would convert the *Oryzomys* karyotype into a near copy of *A. olrogi*. However, we can see no grounds for such a supposition, as *Andalgalomys* is clearly a phyllotine. Its karyotype can be most easily derived from the karyotype of *Calomys sorellus* by a process involving only pericentric inversions (see Fig. 10) or other arm-addition processes. In the absence of contrary data, we prefer this simple explanation of the karyotypic relationships of *Andalgalomys*, particularly because it coincides with our interpretations of morphological relationships. The variation in the known phyllotine karyotypes (Pearson and Patton, 1976) is certainly not much greater than the differences within some genera (for example, *Perognathus*, Patton, 1970; Williams, 1978). Thus, at this point we do not attach any particular importance to the dissimilarity of *A. olrogi* to other phyllotine karyotypes, and doubt that data on comparative gross morphology of the chromosomes of phyllotines are particularly useful for generic groupings when considered alone.

In summary, most of the analyses point to a relatively close relationship between *Calomys*, *Eligmodontia*, and *Andalgalomys*. Dental traits, morphometric analyses, phallic morphology, and karyology are consistent in showing these affinities. We propose that a fairly generalized, dry-grassland or Chaco-dwelling, *Mus*-like Sigmodontini (that is, something like *Calomys*) was the prototype for the phyllotine group. *Andalgalomys pearsoni* has most of the characters that an annectent form between a *Calomys*-like ancestor and the more specialized phyllotines would be expected to exhibit. There is much evidence to support a close relationship between *Calomys* and *Eligmodontia*, although we regard the foot, tooth, and bullar specializations of *Eligmodontia* as sufficiently divergent to warrant generic separation. We see no convincing reasons however, to suggest a *Phyllotis* origin for *Eligmodon-*

tia, as Pearson and Patton (1976) and Gardner and Patton (1976) have done.

The Gran Chaco, or thorn forest, of South America is an extensive, largely uninterrupted habitat, occurring from Brazil through central Argentina. During mesic periods of the Pleistocene, the Chaco was probably even more extensive than today, and intruded into areas that currently support xeric Monte Desert vegetation (the flora of which was largely derived from Chaco ancestors, Morello, 1958). We suggest that during earlier periods of the Pleistocene a form ancestral to *A. olrogi*, and probably similar in morphology to the generalized genus *Calomys*, was a widespread Chacoan species. As Chaco vegetation moved into the valleys of the Monte, this ancestral form was able to invade these areas. When the Chaco vegetation largely withdrew from areas such as the Bolsón de Pipanaco, a relictual population became progressively more adapted to xeric lowland conditions. Its habitat today is fine alluvial soil, supporting *Larrea cuneifolia* and interdigitations of gallery forests (*Cercidium*, *Prosopis*, *Acacia*, *Bulnesia*, and *Opuntia*; see Mares, 1975, 1977*b*; Orians and Solbrig, 1977; Fig. 7).

A. olrogi is relatively specialized for this desert habitat, exhibiting features common to desert-dwelling murids such as its lengthened and pencilled tail, lax pelage, inflated bullae and enlarged auditory pinnae, lengthened hind limbs, and reduced size of the lateral digits. In these features, *A. olrogi* exhibits remarkable convergence with gerbillines such as *Gerbillurus*. The convergence even extends to the development of palatal slits in *A. olrogi* (the slits are individually variable and less well developed in *A. pearsoni*), a feature common to gerbillines, but unknown in New World cricetines.

A. pearsoni is very likely more similar to the ancestral form and possesses more primitive traits than *A. olrogi*. It appears to be a nonforest offshoot of the hypothetical Chaco type, and today is apparently limited to islands of grassland within the Chacoan thorn forest (Myers, 1977). In such a habitat (which may be a persistent subunit of the generalized Chaco habitat) it can probably exist without serious competition from the larger, more arboreal *G. griseoflavus*. We visualize *Graomys* as specializing for exploitation of the thorn scrub and xeric monte habitats, and limiting *A. pearsoni* to intersylvan refugia.

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